Woody vegetation–environment relations in a semi-arid savanna in the northern Transvaal

T.G. O'Connor

De Beers Consolidated Mines Limited, P.O. Box 616, Kimberley, 8300 Republic of South Africa

Present address: Department of Agricultural Development, Private Bag X15, Stutterheim, 4930 Republic of South Africa

Received 8 November 1991; revised 4 May 1992

The relations between gradients in the composition and structure of the woody vegetation and environmental factors, principally substrate type, were investigated with correspondence analysis for an area of 8700 ha of mopane veld in the northern Transvaal. *Colophospermum mopane* was present in all 269 stands sampled, and 46 woody species occurred frequently enough to be included in the analysis. The first ordination axis described a gradient from shrub woodlands with a high abundance of *C. mopane* on colluvial or alluvial soils or exposed calcrete, through to taller woodlands with a lower abundance of *C. mopane* and a greater equitability of other species, occurring on either shallow non-calcareous soils overlying gneisses or schists or on rugged terrain of diabase or marble geology. The second axis separated the different shrub *C. mopane* woodlands on calcrete from those on colluvial or alluvial soils. There were significant differences between substrate types in the abundance of twelve species of the twenty most common species tested.

Die verwantskap tussen gradiënte in die samestelling en struktuur van die houtagtige plantegroei en omgewingsfaktore, hoofsaaklik substraattipe, is vir 'n gebied van omtrent 8700 ha van mopanieveld in die noordelike Transvaal met ooreenstemmingsanalise ondersoek. *Colophospermum mopane* was teenwoordig in al 269 standplase wat ondersoek is, en 46 houtagtige spesies het so dikwels voorgekom dat dit in die analise ingesluit kon word. Die eerste ordenings-as het 'n gradiënt beskryf vanaf struikbosland met 'n hoë voorkoms van *C. mopane* op kolluviale of alluviale gronde of blootgestelde kalkreet, deurlopend na hoër bosland met 'n laer voorkoms van *C. mopane* en 'n groter bydrae van ander spesies wat óf op gneise of skiste bedek met vlak, nie-kalkagtige grond voorgekom het, óf op ongelyke terrein met diabaas- of marmergeologie. Die tweede as het die verskillende struik-*C. mopane*-boslande op kalkkreet geskei van dié op kolluviale of alluviale gronde. Daar was betekenisvolle verskille tussen substraat-tipes in die voorkoms van twaalf van die twintig mees algemene spesies wat ondersoek is.

Keywords: *Colophospermum mopane*, correspondence analysis, substrate.

Introduction

The savanna regions of southern Africa occur within a mean rainfall regime of 300 – 800 mm per annum, within which two major vegetation distinctions are recognized: an arid eutrophic zone and a mesic to moist dystrophic zone (Huntley 1982). At this scale, climate would appear to be the overriding determinant of vegetation structure and composition. The floristic variation within savannas at a regional or local level is strongly influenced by topography and substrate (references cited in Scheepers 1983), and there is usually an associated variation in the structure of the vegetation (*e.g.*, Bredenkamp & Theron 1985). However, topo-edaphic differences at the regional level are confounded by rainfall gradients (*e.g.*, Gertenbach 1983; le Roux *et al.* 1988). At a regional level, the diverse geology (Kent 1980) and hence substrate type of the mopane veld (*sensu* Acocks 1975) of the northern Transvaal influences the vegetation (Louw 1970), but his study covered the entire area north of the Soutpansberg, and was similarly confounded by a rainfall gradient. This study was of a number of contiguous farms which constitute a small section of the region studied by Louw (1970), but contain a complex geology for so small a region.

The objective of this study was to identify whether topography and substrate type, independently of rainfall variation, are important determinants of the composition and structure of the woody vegetation of a semi-arid savanna on a local scale. Only the woody component of the vegetation, rather than the total floristics, has been considered because the composition of the herbaceous component of semi-arid savannas can be completely altered by grazing history, and changes rapidly in response to annual rainfall variability (O'Connor 1985).

Study area

The area (29°15′ – 29°25′E, 22°21′ – 22°30′S) comprises the farms Drumsheugh 99 MS, Elesger 98 MS, Krone 104 MS, Rugen 105 MS (portion) and Venetia 103 MS, totalling approximately 8700 ha. Krone, Rugen and Venetia were first settled in the 1870s, while Drumsheugh and Elesger were first settled in 1941. Farming has been based on cattle, goats and sheep, although dryland cropping has been opportunistically practised on small areas.

The average minimum monthly temperature at Messina (80 km E) ranges from 7.2°C (June, July) to 20.3°C (December), while the average maximum monthly temperature ranges from 24.7°C (June) to 32°C (October, November, December). Frost does not generally occur. The rainfall season is November to March. The mean annual rainfall (July to June) of Alldays (40 km S) is 384 mm (recorded over 48 years), with a 40% coefficient of variation. The annual actual evapotranspiration for Messina is equal to the annual precipitation, and the region experiences a perennial water deficit of 85.6 cm (Schulze 1958).

The area lies in the central zone of the Limpopo Mobile Belt, and includes the southern edge of the more recent Limpopo Karoo sedimentary basin. The older rocks of the mobile belt have suffered several periods of high-grade metamorphism. These metamorphic rocks include an older series of torralitic granite gneisses, as well as a younger series of various gneisses, magnetite quartzites, marbles, amphibolites, granulites and metaquartzites known as the Messina formation. Various basic and ultrabasic rock types ascribed to the Rooiwater and Jamestown igneous suites have been deformed together with the gneisses and Messina formation rocks. The eroded edge of the Karoo sedimentary basin passes irregularly across the area. The basement is successively covered by a sedimentary sequence of conglomerates, grits, sandstones and shales of the Ecca and Beaufort series, overlain by sandstones, marls, mudstones and siltstones of the Stormberg series. The area has been intruded by diabase (pre-Karoo) and dolerite (post-Karoo) dykes, as both irregular bodies and sheets.

The farms of this study are situated in predominantly metamorphic terrain, with an associated complex suite of geological types (Figure 1). The metamorphic rock types of the study area can be grouped into gneisses and schists, metapelites and calc-silicates. Two outliers to the main Karoo sedimentary basin occur, both of coarser materials, and there are a number of prominent diabase intrusions. Most of the diabase dykes have formed pronounced hills.

The area is mapped (Partridge & Maud 1987) as a dissected area under structural control, north of an undifferentiated post-African surface. A basin has been filled with a gritty-silty colluvium (up to 12 m thick), mostly derived from eluvial outwash of Karoo sediments. Alluvium occurs directly adjacent to drainage lines. Surface-exposed calcrete is widespread, and surface calcrete is most commonly a result of calcretization of carbonate-rich meta-sedimentary rocks rather than calcretization within the soil described by Netterberg (1980).

Methods

Data collection

An initial stratification of physiognomic vegetation types was accomplished using aerial photographs. A total of 269 units were delineated, and an area of approximately 2 ha of each of these units was thoroughly inspected (on a plotless basis) and the following information was recorded. The cover of individual species and all species comprised three layers: shrub (<3 m in height), sub-canopy and canopy, and for all layers combined was ranked using a nine-point scale (based on Walker 1976). The cover rankings were 0, + (present but sparse), 1 (1–12%), 2 (13–25%), 3 (26–50%), 4 (51–75%), 5 (76–87%), 6 (88–99%) and 7 (100%). Some of the woody species of smaller stature (<0.5m), for example *Vernonia cinerascens*, *Euphorbia guerichiana* and *Protasparagus* spp., and tree climbers such as *Cissus cornifolia*, *Cissus quadrangularis* or *Sarcostemma viminale*, were not included. *Grewia bicolor* and *Grewia flava* appear to be extensively hybridized (Wild 1984), and were therefore all listed as *G. bicolor*. Nomenclature follows that of Gibbs Russell *et al.* (1987).

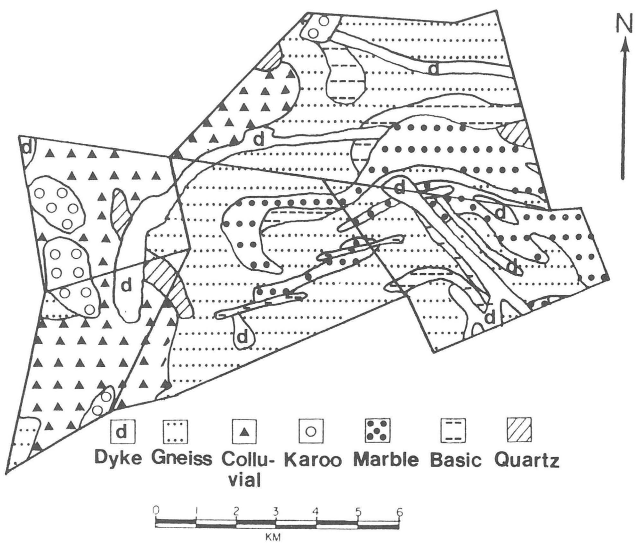

Figure 1 The geological types of the study area. Key to the figure: Karoo – conglomerates, grits, sandstones and shale; Gneiss – gneisses and schists; Basic – various altered basic and ultrabasic rocks, including amphibolites; Quartz – metaquartzite and magnetite quartzite; Marble – marble; Dyke – diabase and dolerite dykes; Colluvial – colluvial outwash. Calcretes, kimberlites and alluvial soils are not shown.

The degree of brokenness of the terrain was ranked on a five-point scale (1 = flat, 5 = precipitous). The percentage of surface rock cover was ranked on a six-point scale with 20% class intervals and 0%. The average height of the tree canopy was estimated to the nearest metre. The substrate type was noted.

Data analysis

Vegetation gradients were assessed by reciprocal averaging (correspondence analysis), using the CANOCO package (Ter Braak 1988). Cover rankings are essentially a logarithmic transformation of an abundance value (Jager & Looman 1987), and species which occurred at a + ranking were set at 0.7. This was necessary to distinguish the uncommon species from the common species which did not occur with a cover ranking greater than 1. Very scarce species (<3 plots, cover = +) were not entered into the analysis. CANOCO allows environmental and structural variables to be analysed concurrently with the vegetation data (Ter Braak 1987, 1988). Substrate type was entered as five nominal variables: (i) colluvial and alluvial soils, (ii) shallow, generally non-calcareous soils overlying gneisses and schists, (iii) calcretized and some basic rocks (mainly amphibolites), (iv) coarse Karoo sandstones and metaquartzites, and (v) diabase and marble extrusions. The terrain, rock cover, vegetation height and cover were entered as recorded.

In the biplot of the species and the environmental variables, rock cover and brokenness are represented by arrows (which point roughly in the direction of maximum variation). The longer an arrow relative to an axis, the greater the correlation of that variable with that axis. The order of the species points projected onto the arrow of an environmental variable, corresponds approximately to the weighted averaging of the species with respect to the environmental variable. Each of the five nominal variables for substrate type are represented by a point located at the centroid of the sample scores belonging to that class. A weighted multiple regression of the sample scores for each ordination axis on the standardized environmental variables was computed. Regression coefficients were derived from the weighted least-squares fit of the model (t-value tested against critical t with n–q–1 d.f., where n is the number of samples and q the number of variables).

Because of the influence of substrate on the variation in the composition and structure of the woody vegetation (see the Results section), the influence of substrate on the abundance of twenty of the more common species and on the cover and height of the vegetation, and on the cover of each of the strata, was examined in greater detail. Differences between substrates in the abundance of *C. mopane*, total cover and height were examined with one-way ANOVA with Tukey's studentized range test to test for differences between means. The cover rankings were used as a response variable. The other species rarely had cover rankings greater than one, and therefore the differences in the frequency of occurrence of each species on the different substrates were examined with G-tests (Sokal & Rohlf 1981).

Results

Vegetation gradients

The eigenvalues of the first four axes of reciprocal averaging were 0.250, 0.158, 0.128 and 0.113, respectively, indicating that vegetation gradients existed, but were not pronounced. The site scores of the first and second axes ranged over 3.17 and 2.51, respectively, indicating a limited amount of compositional turnover. The ordination revealed no marked outlier sites. The cumulative percentage variance accounted for by the first four axes of the species–environment biplot was high, namely 43.1, 54.5, 59.3 and 65.4%. Hence the first two axes are considered an adequate representation of the species and environmental variables (Figure 2).

The proportion of the total variance in the standardized environmental data extracted by each species axis was low: 0.113 (axis 1), 0.035 (axis 2), 0.022 (axis 3) and 0.045 (axis 4). Certain well-defined correlations existed within the suite of environmental variables (only correlations of $p < 0.05$ are quoted). More bouldery areas tended to be more broken (r = 0.71), and were primarily associated with diabase/marble geology (r = 0.53). Brokenness was most strongly correlated with sandstone/quartzite geology (r = 0.38). The colluvial/alluvial substrate (coefficient = 0.29, t = 5.51) and the calcrete substrate (coefficient = 0.38, t = 6.21) contributed significantly to the regression for the first axis, whereas the calcrete substrate (coefficient = 0.15, t = 2.51), the colluvial/alluvial substrate (coefficient = 0.13, t = 2.49) and the

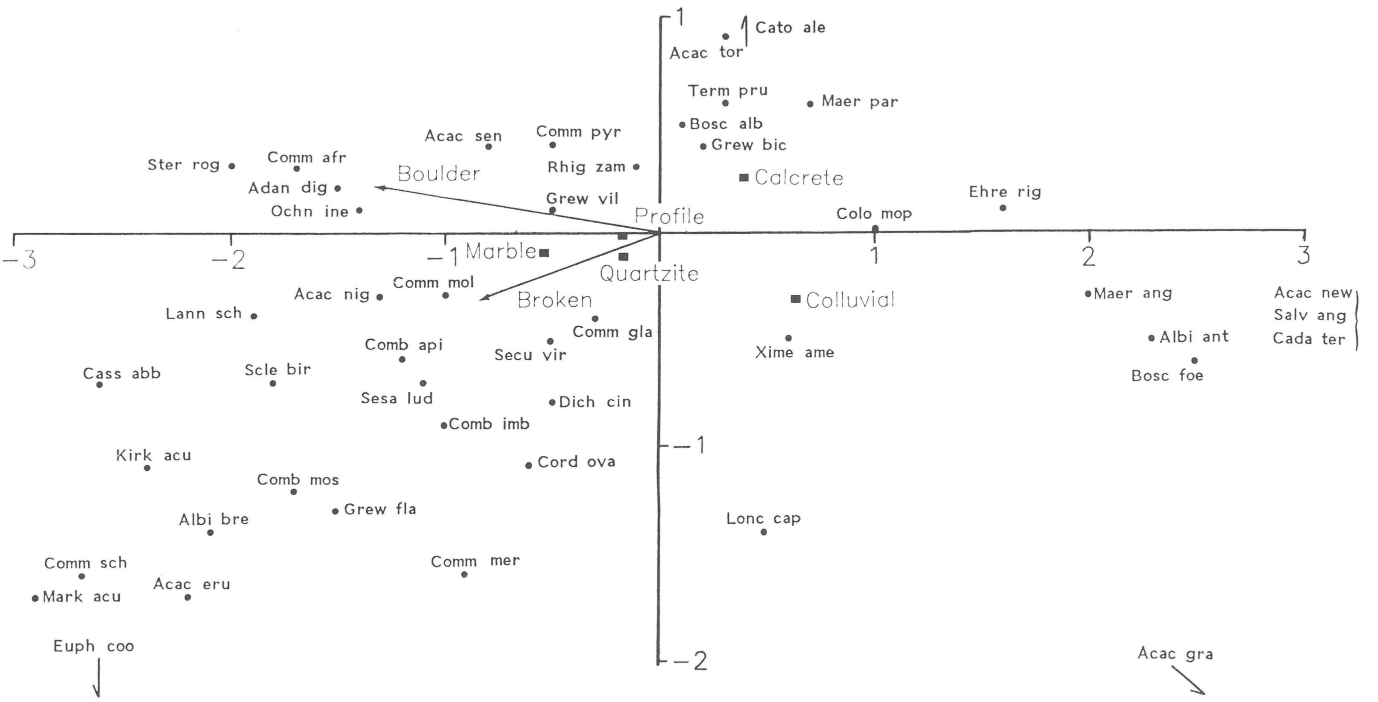

Figure 2 A biplot of the species scores and the environmental variables of the first two ordination axes. The centroids of the substrate types are denoted as squares. The scale of the arrows is $\times 10^{-1}$. Notation for species: Acac eru – *Acacia erubescens*; Acac gra – *Acacia grandicornuta*; Acac new – *Acacia newbrownii*; Acac nig – *Acacia nigrescens*; Acac sen – *Acacia senegal* var. *leiorachis*; Acac tor – *Acacia tortilis*; Adan dig – *Adansonia digitata*; Albi ant – *Albizia anthelmintica*; Albi bre – *Albizia brevifolia*; Bosc alb – *Boscia albitrunca*; Bosc foe – *Boscia foetida* subsp. *rehmanniana*; Cada ter – *Cadaba termitaria*; Cass abb – *Cassia abbreviata*; Cato ale – *Catophractes alexandri*; Colo mop – *Colophospermum mopane*; Comb api – *Combretum apiculatum*; Comb imb – *Combretum imberbe*; Comb mos – *Combretum mossambicense*; Comm afr – *Commiphora africana*; Comm gla – *Commiphora glandulosa*; Comm mer – *Commiphora merkerii*, Comm mol – *Commiphora mollis*; Comm pyr – *Commiphora pyracanthoides*; Comm sch – *Commiphora schimperi*; Cord ova – *Cordia ovalis*; Dich cin – *Dichrostachys cinerea*; Ehre rig – *Ehretia rigida*; Euph coo – *Euphorbia cooperi*; Grew bic – *Grewia bicolor*; Grew fla – *Grewia flavescens*; Grew vil – *Grewia villosa*; Kirk acu – *Kirkia acuminata*; Lann sch – *Lannea schweinfurthii*; Lonc cap – *Lonchocarpus capassa*; Maer ang – *Maerua angolensis*; Maer par – *Maerua parvifolia*; Mark acu – *Markhamia acuminata*; Ochn ine – *Ochna inermis*; Rhig zam – *Rhigozum zambeziacum*; Salv ang – *Salvadora angustifolia*; Scle bir – *Sclerocarya birrea*; Secu vir – *Securinega virosa*; Sesa lud – *Seasamothamnus lugardii*; Ster rog – *Sterculia rogersii*; Term pru – *Terminalia prunioides*; Xime ame – *Ximenia americana*.

brokenness of the terrain (coefficient = –0.13, t = 3.54) contributed significantly to the regression for the second axis. None of the variables contributed significantly to the regression for the third axis.

The environmental correlates of the first floristic axis were diabase/marble substrate (r = –0.50), calcrete substrate (r = 0.45), boulder cover (r = –0.31) and colluvial/alluvial soils (r = 0.40). The environmental correlates of the second floristic axis were calcrete (r = 0.38) and colluvial/alluvial substrate (r = –0.27). Canopy cover and canopy height (r = 0.49) were negatively correlated with the first floristic axis (r = –0.30 and –0.48, respectively), whereas shrub cover and total cover (r = 0.76) were positively correlated with this axis (r = 0.37 and 0.34, respectively). The third species axis showed no clear correlation with any of the structural variables.

Shrub cover (and total cover) were positively correlated with the degree of brokenness (r = 0.34), sandstone/quartzite geology (r = 0.23), calcrete areas (r = 0.21) and colluvial soils (r = 0.18), and negatively correlated with diabase/marble substrate (r = –0.25) and with shallow non-calcareous soils (r = –0.23). Canopy cover (and canopy height) was positively correlated with a diabase/marble substrate (r = 0.33) and negatively correlated with calcrete (r = –0.35). Cover of the sub-canopy layer showed no correlations with any of the environmental variables.

The first axis clearly described a gradient from stands with a low species richness and a high cover of *C. mopane* (predominantly shrubs), associated with calcrete or colluvial or alluvial substrates, to stands with a higher species richness and a lower cover of *C. mopane*, with a prominent and moderately tall canopy layer, associated with a substrate of diabase, marble, sandstone, metaquartzite or a developed soil overlying gneisses or schists. Although *C. mopane* occurred with a 100% frequency, the species was clearly identifiable with the centroids of the calcrete and the colluvial/alluvial substrates (Figure 2). Only seven other species are associated with these latter substrate types, whereas a host of species are associated with the other group of substrate types. However, the centroids of the diabase/marble, sandstone/metaquartzite and developed profile substrate types are all in close proximity, indicating that the majority of these species were equally associated with each of them.

The second axis (Figure 2) separated the group of stands with characteristically dense *C. mopane* shrub woodland into those on a calcrete substrate and those on alluvial or colluvial soils. *Albizia anthelmintica, Maerua angolensis, Boscia foetida, Acacia grandicornuta, A. newbrownii, Salvadora angustifolia* and *Cadaba termitaria* are closely associated with a colluvial or alluvial substrate, while *Maerua parvifolia*, and to a lesser extent *Grewia bicolor, Terminalia prunioides* and *Boscia albitrunca* are associated with a calcrete substrate. *Ehretia rigida* was an infrequent species on both substrates. The second axis also separated out *Commiphora pyracanthoides* and *Rhigozum zambeziacum*, which were more closely associated with a developed soil profile. Species indicative of a high rock cover include *Sterculia rogersii, Commiphora africana, Adansonia digitata, Markhamia acuminata, Cassia abbreviata* and *Kirkia acuminata*, whereas the latter three mentioned, together with *Acacia erubescens* and *Albizia brevifolia*, were indicative of very broken terrain (Figure 2). Little can be inferred about the environmental relations of *Commiphora schimperi, Euphorbia cooperi* or *Catophractes alexandri* because of their rarity, indicated by their outlier positions (Figure 2).

The differences between substrates in the abundance of twenty common species and of vegetation height and cover are summarized in Table 1. Although *C. mopane* occurred on all sites, its abundance differed between substrates (Table 1). The cover of *C. mopane* was highest on the colluvial/alluvial soils, and progressively lower on the calcrete, sandstone/metaquartzite, developed soil profiles and diabase/marble substrates. There were no differences between substrates in the frequency of occurrence of *Terminalia prunioides, Boscia albitrunca, Rhigozum zambeziacum, Grewia villosa, Grewia bicolor* or *Ximenia americana. Combretum apiculatum* occurred infrequently on the colluvial/alluvial soils and the calcrete areas, but was widespread on the rocky sandstone/metaquartzite, developed soil profile and diabase/marble areas. *Commiphora glandulosa* was most common on the diabase/marble and developed soil profile areas and infrequent on calcrete areas. *Dichrostachys cinerea* was relatively common on all substrate types except calcrete. *Commiphora pyracanthoides* and *Commiphora mollis* were similarly distributed in that both were most common on diabase/marble, developed soil profile and sandstone/metaquartzite areas and least common on calcrete areas, but differed in that *C. mollis* was not as common on colluvial/alluvial soils. *Maerua parvifolia* tended to be far more common on the calcrete areas. *Acacia tortilis* was most common on developed soil profiles, colluvial and calcrete areas, and least common on diabase/marble and sandstone/metaquartzite areas. *Boscia foetida* and *Ehretia rigida* were most common on colluvial and calcrete substrates and infrequent or absent from the others. *Lannea schweinfurthii, Acacia nigrescens* and *Sclerocarya birrea* were common on diabase/marble substrates, relatively common on developed profile and sandstone/metaquartzite substrates, but scarce on colluvial or calcrete substrates. *Cordia ovalis* occurred most commonly on diabase/marble and colluvial substrates.

The substrates differed in their total vegetation cover, vegetation height, canopy cover, mid-stratum cover and shrub cover (Table 1). The pattern of differences for shrub cover and total cover were very similar: both were equivalent on the diabase/marble and developed profile areas, and were lower than the other three substrates which did not differ. In contrast, the cover of the canopy and the vegetation height were highest on the diabase/marble substrate and lowest on calcrete areas.

Discussion

The floristic and structural character of the woody vegetation was strongly influenced by topo-edaphic conditions, reflected in the environmental and vegetation structural correlates of the ordination (Figure 2), and the significant effect of substrate on the abundance of the most common species (Table 1). Geologically, the area is extremely complex for so small a region (Figure 1). Topo-edaphic regulation of floristic variation appears to be a characteristic feature of southern African savannas, for example in Etosha National Park (le Roux *et al.* 1988), the southern Kalahari

Table 1 The values for five substrate types of (i) the percentage cover of *C. mopane*, (ii) the percentage cover of canopy, mid-stratum, shrub and total cover, and vegetation height, and (iii) the percentage frequency of occurrence of nineteen of the more common woody species†

		Substrate type				
Variable	Colluvial $n = 30$	Calcrete $n = 92$	Diabase $n = 45$	Profile $n = 68$	Sandstone $n = 33$	F or G value
(i) *C. mopane* cover (%)	55^{a}	40^{b}	12^{d}	23^{c}	29^{bc}	26.3***
(ii) Total cover (%)	72^{a}	63^{a}	54^{b}	52^{b}	66^{a}	10.5***
Shrub cover (%)	47^{a}	40^{a}	26^{b}	28^{b}	44^{a}	12.5***
Mid-stratum cover (%)	17^{a}	8^{c}	15^{ab}	13^{bc}	12^{bc}	5.6***
Canopy cover (%)	15^{ab}	9^{c}	17^{a}	11^{b}	12^{b}	16.4***
Height (m)	6.2^{b}	4.5^{d}	7.2^{a}	6.3^{b}	5.2^{c}	43.2***
(iii) *Acacia nigrescens* (%)	13	18	82	15	33	31.2***
Acacia tortilis (%)	57	47	24	65	24	14.9***
Boscia albitrunca (%)	80	91	91	90	97	0.5
Boscia foetida (%)	63	35	0	6	12	45.4***
Combretum apiculatum (%)	30	24	82	79	91	42.7***
Commiphora glandulosa (%)	43	27	58	54	36	10.4*
Commiphora mollis (%)	37	39	87	72	76	18.3***
Commiphora pyracanthoides (%)	67	42	91	81	67	14.9***
Cordia ovalis (%)	20	7	22	4	12	10.0*
Dichrostachys cinerea (%)	57	21	58	66	58	24.3***
Ehretia rigida (%)	20	27	7	10	6	11.8*
Grewia bicolor (%)	87	96	98	90	94	0.4
Grewia villosa (%)	3	11	29	9	12	9.5
Lannea schweinfurthii (%)	17	13	82	37	55	32.2***
Maerua parvifolia (%)	60	89	62	56	67	7.4
Rhigozum zambeziacum (%)	17	29	36	24	24	2.4
Sclerocarya birrea (%)	17	9	80	47	45	39.3***
Terminalia prunioides (%)	77	99	100	85	88	1.9
Ximenia americana (%)	80	64	67	46	73	5.5

† The same superscripts (within a row) for sections (i) and (ii) denote substrate types which are not significantly different ($p > 0.05$) using Tukey's studentized range test.

*** $p < 0.001$.

* $p < 0.05$.

(Werger *et al.* 1979), the Kruger National Park (Fraser *et al.* 1987) and the Klaserie Nature Reserve (Witkowski 1983).

A striking feature of the area was the ubiquitous occurrence of *C. mopane* in all the plots sampled, on substrates ranging from calcrete sheets to deep colluvial soils. The major gradient of the ordination was strongly influenced by the abundance of this species. The distribution of *Colophospermum mopane* is probably related to climatic factors at a sub-continental level (Henning 1976), but this species characteristically occurs on a wide array of substrate types at a regional or local level, often forming almost monospecific stands. In the mopane veld of the northern Transvaal (of which the study area forms a part), *C. mopane* has a low ecological status and is found in most environments (Louw 1970). Similarly, the species is a predominant component of most of the wooded vegetation types of the Etosha National Park, occurring on lithosols, on coarsely fractured calcrete, calcified dolomite or low-grade marble, hilly andesite areas, and shallow Kalahari sands (le Roux *et al.* 1988). The species is similarly widespread over diverse substrate types in the Kruger National Park (Gertenbach 1983). In the northern Kruger National Park, *C. mopane* is the principal species of a number of communities found on alluvium, shale, basalt, andesite and the Malvernia formation (van Rooyen *et al.* 1981). The overall vegetation structure varied according to substrate, for example, clays derived from Karoo basalts supported a shrub savanna while alluvium supported a tree savanna (van Rooyen *et al.* 1981).

The distribution of *Combretum apiculatum* on the substrate types of this study area paralleled the distribution of the species in the Kruger National Park (Fraser *et al.* 1987) and the adjacent Klaserie Reserve (Witkowski 1983). In the latter two areas the species was predominant on the acidic coarser textured soils (skeletal to deep) derived from granite gneisses, and on rocky soils. The common association of *Terminalia prunioides* with *C. mopane* woodlands has also been noted in Etosha National Park (le Roux *et al.* 1988) and in the drier *C. mopane* woodlands of the Kruger National Park (Gertenbach 1983). Many of the species characteristic of the bouldery and broken areas of diabase/marble geology (Figure 2), for example *Kirkia acuminata* and *Sterculia rogersii*, are also common in the drier and rugged broken landscapes of the Kruger National Park (Gertenbach 1983). *Acacia nigrescens, Sclerocarya birrea* and *Lannea schweinfurthii* were similar in their distribution, and notably were almost absent from calcrete or alluvial or colluvial substrates.

There are few areas in the northern Transvaal with so much exposed calcrete. Although *Catophractes alexandri* is a recognized calciphilous species and an indicator of subsurface calcrete in the Kalahari (Netterberg 1980), the species was absent from nearly all of the calcrete areas of this study, and was distributed in a very clumped fashion. *Acacia senegal* var. *leiorachis* was also distributed in a very clumped fashion, and the environmental relationships of these two species in this study area are unclear. Although *Boscia foetida* subsp. *rehmanniana* was identified as having an affinity for colluvial or calcrete substrates, observation suggested that the distribution of this species within areas of these substrates was very specific. This species appeared to occur only within certain sub-habitats, for example, the outwash areas of calcrete slopes rather than on the rocky calcrete substrate. In the mopane veld of the northern Transvaal, *B. foetida* had the most pronounced environmental requirements of all the tree and shrub species (Louw 1970). Louw (1970) also found that *Maerua parvifolia* had a preference for higher pH substrates, which conferred with the preference for calcrete areas found in this study.

Variation in the structure of the vegetation was strongly influenced by the variation in the growth habit of *C. mopane* because of the abundance of this species. The growth form of *C. mopane* varied from a multiple-stemmed shrub to single-stemmed trees. Dense stands of *C. mopane* shrub occurred on two very dissimilar substrate types, namely colluvial soils and areas of surface calcrete, while single-stemmed trees were common on non-calcareous soils overlying gneisses and schists. Similarly, in the Kruger National Park, the shrub form is found on fine-textured soils derived from base-rich rocks (basalts, diabase and olivine gabbro) while sandy soils support single-stemmed trees (Fraser *et al.* 1987).

Austin and Smith (1989) drew attention to the location-specific nature of vegetation–environment studies which emphasize indirect environmental variables (*e.g.* substrate, rockiness) rather than environmental variables which are either direct resources for plants (*e.g.* moisture, nutrients) or directly affect plant physiological functioning (*e.g.* temperature, pH). The constraint of studies (such as this one) of indirect variables is that the results cannot necessarily be extrapolated to other geographic areas because the indirect variables may not provide a consistent indicator of direct variables. However, this constraint is to some extent alleviated in the study of substrate–vegetation relations in southern African savannas because of the wide diversity of parent geology in southern Africa and the pronouncedly different soil physico-chemical environments arising from different geological types. This is partly evident from the foregoing discussion of the consistent association between substrate types and certain species over geographically widely separated areas. Therefore, indirect environmental variables have provided a convenient initial focus of research effort in this study.

Acknowledgements

A. van Zyl motivated for this study to be done. I am grateful to P. Williamson for providing part of the summary of the geology, and to K. Prakke for the provision of unpublished information. I thank W.N. Ellery and G.A. Pickett for comment on an initial draft of the manuscript.

References

ACOCKS, J.P.H. 1975. Veld types of South Africa. *Mem. bot. Surv. S. Afr.* 40: 1 – 128.

AUSTIN, M.P. & SMITH, T.M. 1989. A new model for the continuum concept. *Vegetatio* 83: 35 – 47.

BREDENKAMP, G.J. & THERON, G.K. 1985. A quantitative approach to the structural analysis and classification of the vegetation of the Manyeleti Game Reserve. *S. Afr. J. Bot.* 51: 45 – 54.

FRASER, S.W., VAN ROOYEN, T.H. & VERSTER, E. 1987. Soil–plant relationships in the central Kruger National Park. *Koedoe* 30: 19 – 34.

GERTENBACH, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe* 26: 9 – 121.

GIBBS RUSSELL, G.E., WELMAN, W.G., RETIEF, E., IMMELMAN, K.L., GERMISHUIZEN, G., PIENAAR, B.J., VAN WYK, M., NICHOLAS, A., DE WET, C., MOGFORD, J.C. & MULVENNA, J. 1987. List of species of southern African plants. *Mem. bot. Surv. S. Afr.* 56: 1 - 270.

HENNING, A.C. 1976. A study of edaphic factors influencing the growth of *Colophospermum mopane* (Kirk ex Benth) Kirk ex J. Leonard. PhD thesis, University of the Witwatersrand, Johannesburg.

HUNTLEY, B.J. 1982. Southern African savannas. In: Ecology of Tropical Savannas, eds. B.J. Huntley & B.H. Walker. Springer-Verlag, Berlin, Heidelberg.

JAGER, J.C. & LOOMAN, C.W.N. 1987. Data collection. In: Data analysis in community and landscape ecology, ch. 2, eds. R.H.G. Jongman, C.J.F. ter Braak & O.F.R. van Tongeren. Pudoc, Wageningen.

KENT, L.E. (compiler). 1980. Stratigraphy of South Africa, Part 1. Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia and the republics of Bophuthatswana, Transkei and Venda. *Handb. geol. Surv. S. Afr.* 8.

LE ROUX, C.J.G., GRUNOW, J.O., MORRIS, J.W., BREDENKAMP, G.J. & SCHEEPERS, J.C. 1988. A classification of the vegetation of the Etosha National Park. *S. Afr. J. Bot.* 54: 1 – 10.

LOUW, A.J. 1970. An ecological study of mopani veld north of the Soutpansberg. DSc (Agric.) thesis, University of Pretoria.

NETTERBERG, F. 1980. Geology of southern African calcretes: 1. Terminology, description, macrofeatures, and classification. *Trans. geol. Soc. S. Afr.* 83: 255 – 283.

O'CONNOR, T.G. 1985. A synthesis of long term experiments concerning the grass layer of southern African savannas. *S. Afr. Nat. Sci. Prog. Rep.* No. 114.

PARTRIDGE, T.C. & MAUD, R.R. 1987. Geomorphic evolution of southern Africa since the Mesozoic. *S. Afr. J. Geol.* 90: 179 – 208.

SCHEEPERS, J.C. 1983. Progress with vegetation studies in South Africa. *Bothalia* 4: 683 – 690.

SCHULZE, B.R. 1958. The climate of South Africa according to Thornthwaite's rational classification. *S. Afr. Geog. J.* 40: 31 – 53.

SOKAL, R.R. & ROHLF, F.J. 1981. Biometry. W.H. Freeman & Co., New York.

TER BRAAK, C.J.F. 1987. Ordination. In: Data analysis in community and landscape ecology, ch. 5, eds. R.H.G. Jongman, C.J.F. ter Braak & O.F.R. van Tongeren. Pudoc, Wageningen.

TER BRAAK, C.J.F. 1988. CANOCO - a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Tech. Rep. 87 ITI A 11, TNO Inst. of Appl. Computer Sci., Wageningen.

VAN ROOYEN, N., THERON, G.K. & GROBBELAAR, N. 1981. A floristic description and structural analysis of the plant communities of the Punda Milia–Pafuri–Wambiya area in the Kruger National Park, Republic of South Africa: 3. The *Colophospermum mopane* communities. *Jl S. Afr. Bot.* 47: 585 – 626.

WALKER, B.H. 1976. An approach to the monitoring of changes in the composition and utilisation of woodland and savanna vegetation. *S. Afr. J. Wildl. Res.* 6: 1 – 32.

WERGER, M.J.A., MORRIS, J.W. & LOUPPEN, J.M.W. 1979. Vegetation–soil relationships in the southern Kalahari. *Docums Phytosociol.* 4: 967 – 981.

WILD, H. 1984. Flora of southern Africa, Vol. 21, Part 1, *Tiliaceae*, ed. O.A. Leistner. Botanical Research Institute, Department of Agriculture, Pretoria.

WITKOWSKI, E.T.F. 1983. Ecology of the Klaserie Private Nature Reserve. MSc thesis, University of the Witwatersrand, Johannesburg.